BOREOPRICEA FROM THE LOWER TRIASSIC OF RUSSIA, AND THE RELATIONSHIPS OF THE PROLACERTIFORM REPTILES

by MICHAEL J. BENTON *and* JACKIE L. ALLEN

ABSTRACT. *Boreopricea funerea* from the Lower Triassic of northern Russia is a prolacertiform diapsid, superficially similar to *Prolacerta* from the Lower Triassic of South Africa. The skull is damaged, but relatively complete. The lower temporal bar is absent. Some parts of the skeleton of *Boreopricea*, in particular some of the vertebrae and the foot, are well preserved, and offer clear evidence of prolacertiform affinities. Nineteen species of prolacertiform have been described. Their affinities are difficult to resolve because available specimens for many of the taxa are incomplete. A series of cladistic analyses shows the existence of a tanystropheid clade (*Tanystropheus*, *Tanytrachelos*), to which are allied *Cosesaurus*, *Malerisaurus*, *Boreopricea*, and *Macrocnemus* as successive outgroups. A new synapomorphy of prolacertiforms may be the tight association of astragalus, calcaneum, centrale, and distal tarsal 4 in the ankle, with the centrale in contact with the tibia.

BOREOPRICEA funerea was erected by Tatarinov (1978) on the basis of a single complete skull and skeleton of a small reptile from the Lower Triassic of Arctic Russia. Tatarinov (1978) identified *Boreopricea* as a 'prolacertilian' and a member of the family Prolacertidae. Since then, systematists (Benton 1985; Evans 1988) have assumed that this genus was a prolacertiform, and it has been assigned a position in cladograms close to *Prolacerta* and *Macrocnemus*.

The purpose of this paper is to describe *Boreopricea*, to illustrate the material, to clarify some details of its anatomy, and to consider its relationships. This redescription is necessary since Tatarinov's (1978) description was incomplete, poorly illustrated, and incorrect in parts.

Institutional abbreviation. PIN, Palaeontological Institute, Moscow.

SYSTEMATIC PALAEONTOLOGY

Class DIAPSIDA Osborn, 1903
Superdivision NEODIAPSIDA Benton, 1985
Division ARCHOSAUROMORPHA von Huene, 1946
Order PROLACERTIFORMES Camp, 1945
Family PROLACERTIDAE Parrington, 1935

Genus BOREOPRICEA Tatarinov, 1978

Boreopricea funerea Tatarinov, 1978

Text-figures 2–15

Holotype. PIN 3708/1, a nearly complete skull and skeleton, lacking the pelvis, the posterior dorsal vertebrae and anterior caudals; collected in 1972 by the Nenetska (Region) Geological Party, from Kolguyev Island, Arkhangel Province, Arctic Russia (49°E 68°S), Borehole No. 141 at 1112.3 m depth (Text-fig. 1); Vetluzhian Series, Induan, Lower Triassic.
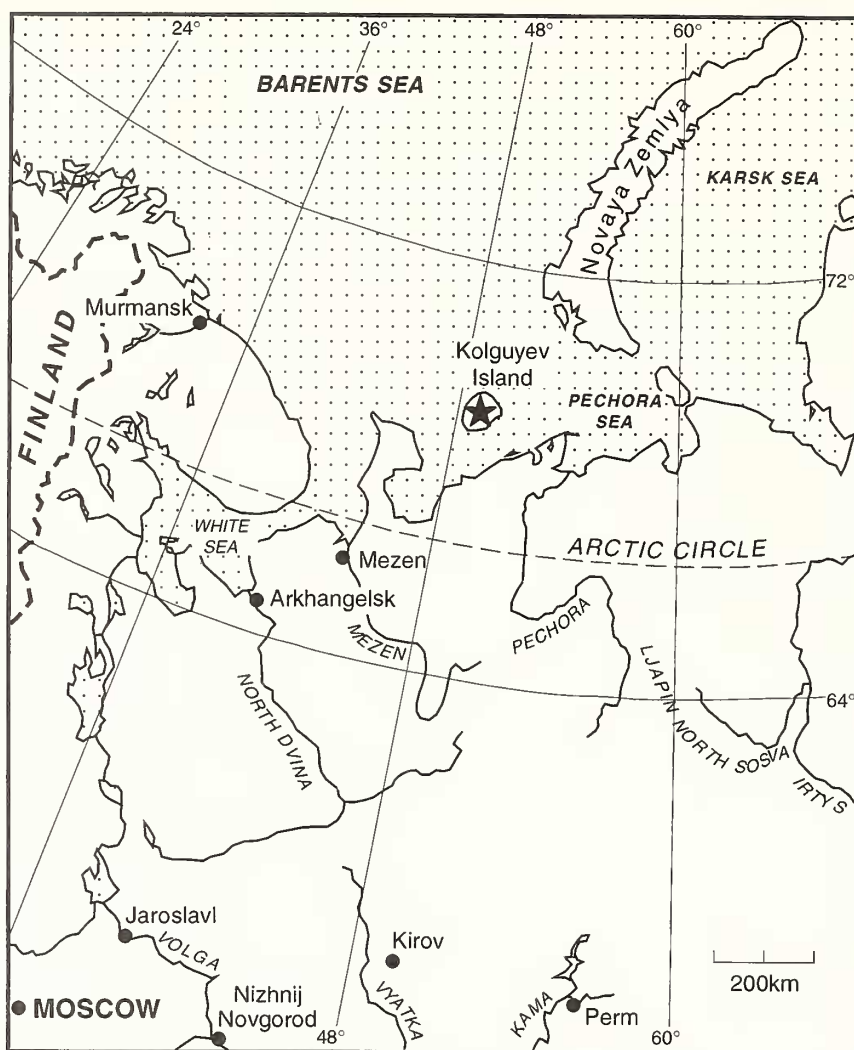
TEXT-FIG. 1. Map of the northern region of the Russian Platform and the Arctic coastline, showing location of the find of *Boreopricea* on Kolguyev Island.

Other material. Tatarinov (1978, p. 511) indicated the existence of a second specimen, PIN 3708/2, 'the anterior end of the muzzle', but this specimen could not be located for the present study.

Diagnosis. A prolacertiform, characterized uniquely by a jugal-squamosal contact. Other synapomorphies: straight fronto-parietal suture; posterior process on jugal absent; quadratojugal tall and with reduced anterior process; posterior dentary teeth lie anterior to posterior maxillary teeth; more than seven cervical vertebrae; metacarpal 3 is equal in length to, or longer than, metacarpal 4; foramen between astragalus and calcaneum absent; second phalanx on digit 5 of foot is long compared with other phalanges. Each of these synapomorphies is shared by other prolacertiforms, but no other taxon has the same character combination.

TEXT-FIG. 2. Type skeleton of *Boreopricea funerea* Tatarinov, 1978 (PIN 3708/1), as currently curated, mounted on card. Pencil outlines indicate bones that are now missing. Scale bar represents 10 mm.
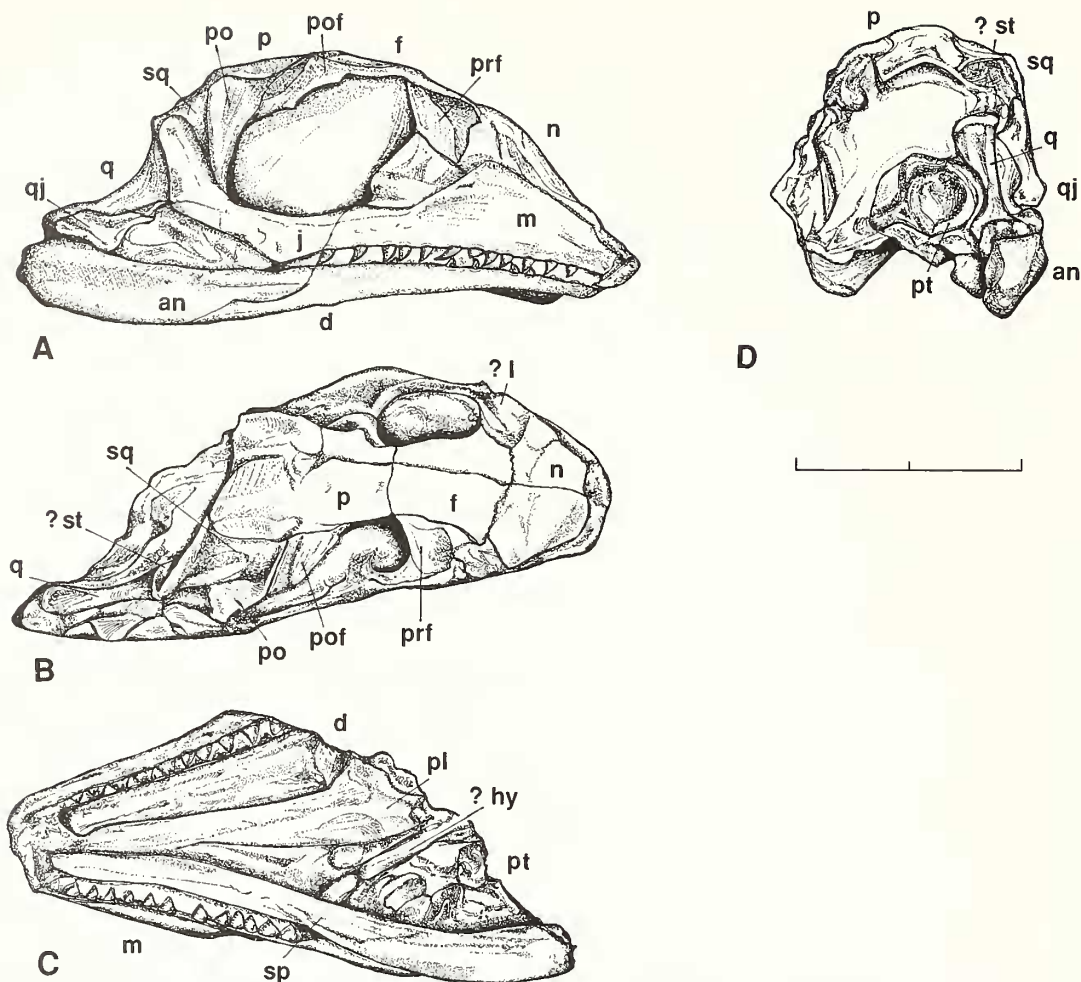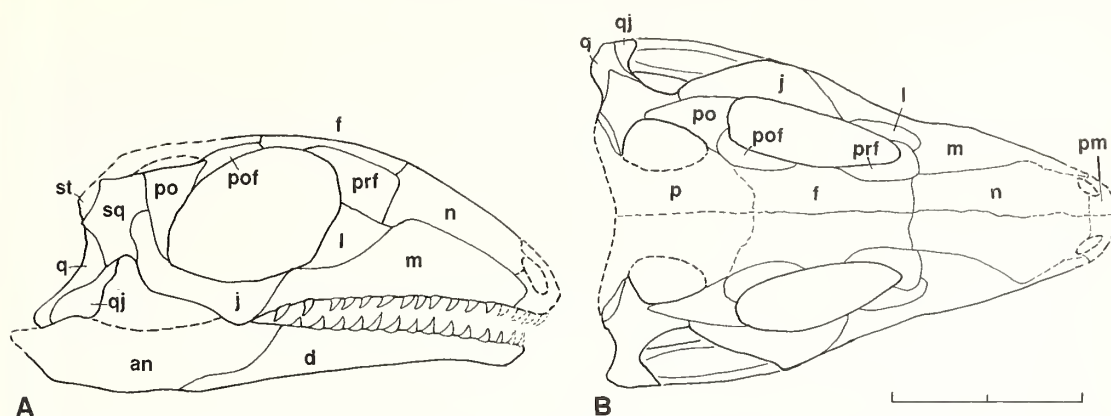
TEXT-FIG. 3. *Boreopricea funerea* Tatarinov, 1978. Skull of PIN 3708/1, as originally preserved, drawn from casts, in right lateral (A), dorsal (B), ventral (C), and occipital (D) views. Abbreviations: an, angular; d, dentary; f, frontal; hy, hyoid element; j, jugal; l, lacrimal; m, maxilla; n, nasal; p, parietal; pl, palatine; po, postorbital; pof, postfrontal; prf, prefrontal; pt, pterygoid; q, quadrate; qj, quadratojugal; sp, splenial; sq, squamosal; st, supratemporal. Scale bar represents 10 mm.

Description

General. The type specimen (Text-fig. 2) is rather less complete than indicated in Tatarinov's (1978) description, since some damage has occurred since then (I. V. Novikov, pers. comm. to MJB, 1993). The specimen was prepared out of the matrix by M. F. Ivakhenko, and the perfectly preserved individual bones of the skeleton were attached to a piece of card in natural arrangement, according to their locations in the rock. Since the time of preparation, the skull has been crushed flat, hence obscuring some detail of bone contacts, and certain elements of the postcranial skeleton have been removed from the card, and some have been lost. A plaster cast of the skull indicates its original uncrushed condition, and this was used as a basis for the illustrations (Text-figs 3–4). Where possible, bones were removed from the card for study on all sides.

Measurements of the skeleton indicate a total length of 440 mm, composed of a 29 mm long skull (tip of snout missing), a presacral column length of 170 mm, an estimated sacral length of (?) 10 mm, and a tail length of 230 mm. The estimates of lengths of portions of the vertebral column are based on the limited evidence of the sporadically preserved vertebrae combined with measurements determined from the arrangement of the

TEXT-FIG. 4. *Boreopricea funerea* Tatarinov, 1978. Reconstruction of skull, based on PIN 3708/1, in lateral (A) and dorsal (B) views. Unknown regions, shown by dashed lines, are based on *Prolacerta*. Scale bar represents 10 mm.

elements on the specimen card. These measurements are rather less than those given by Tatarinov (1978, p. 511), who indicated a skull length of 36 mm and a total length of about 450 mm.

Skull. The skull (Text-figs 3–4) is complete, except for the tip of the snout, the left cheek region, and most of the occiput (braincase, posterior part of parietals, posterior part of left mandibular ramus). The lower jaws are in natural articulation. The orbit is large, and the bones surrounding it may be distinguished on the right in the cast, although they are a little displaced. There appear to be two temporal fenestrae, a small upper one, and a lower one bounded on three sides, but with an incomplete lower temporal bar. Only the posterior margin of the nares can be distinguished, where they are bounded by the nasal and the premaxilla, but the nasals are crushed down on to the top surface of the palate, thus obscuring some detail.

There is no trace of the premaxillae, either in the specimen or in the cast of its original condition, although Tatarinov (1978, p. 508) describes these elements. The remainder of the series of paired midline bones of the dermal skull roof is more clearly seen (Text-fig. 3A–B). The nasals are broad elongate elements, shorter and broader than the slender frontals, which are about 1·2 times the length of the nasals. At the anterolateral margin of each nasal is an elongate rounded excavation, representing part of the posterior margin of the naris. Nasals and frontals are quadratic elements, and a short lateral margin of each frontal enters the margin of the orbit. Only the anterior part of the (?) fused parietals may be seen, and there is no indication of a parietal foramen. Postparietals and tabulars are not preserved. A possible supratemporal on the right-hand side is a narrow displaced element behind the upper temporal fenestra, running from the margin of the parietal to the contact of the quadrate and squamosal. Tatarinov (1978, p. 508) records details of the ventral surfaces of the dermal skull roofing elements, and of occipital elements, but none of these may be seen now in the specimen, or in the cast.

The maxilla (m, Text-fig. 3A–C) is a long bone forming the side of the snout, rising to a rounded high point in front of the orbit, and extending back to contact the jugal. Both maxillae can be seen to bear teeth, and there are marked blood vessel/nerve pits on the surface of the bone above the tooth row. The jugal (j, Text-fig. 3A) is lost from the specimen now, and can be seen only in the cast. It is a boomerang-shaped element in the lower posterior angle of the orbit, and it shows no sign of a posterior process beneath the lower temporal fenestra, merely an oblique angulation. This angle is smooth, and does not appear to be broken. Unusually for reptiles, the jugal appears to contact the squamosal with an elongate process (Text-figs 3A, 4), instead of being separated by the postorbital.

The prefrontal is a small crescent-shaped element in the anterior angle of the orbit, seen only on the right in the cast (prf, Text-fig. 3A–B), but now missing from the specimen. The bone is displaced downwards from its original position, and shows the process that lay under the frontal. The lacrimal is not clear on the right-hand side, but may be indicated by the flat area in the lower anterior angle of the orbit below the prefrontal. An indication of the lacrimal duct may be detected here. On the left-hand side of the cast, a complex structure in the anterior part of the orbital margin is probably composed largely of the lacrimal and its process to the palatine.

The right postfrontal is a displaced triangular slip of bone (pof, Text-fig. 3A–B), showing a long contribution to the posterodorsal orbital margin, and contacting the postorbital. The left postfrontal is crushed. The right postorbital is a triangular element, a little larger than the postfrontal, and with a curved orbital margin, a short posterior process which touches the squamosal, and a long contact with the jugal, clearly seen in the cast because of the displacement (po, Text-fig. 3A–B). The left postorbital may be represented by a curved element that is displaced medially, and seen in the cast, but not now in the specimen.

The elements of the posterior angle of the skull may be seen only on the right-hand side (Text-fig. 3A–B, D). The squamosal is a rectangular flat element that lacks evident processes. The quadratojugal is a small triangular bone slip, with no sign of an anterior process below the lower temporal fenestra. The quadrate is a narrow oblique element which extends from an expanded dorsal contact with the squamosal (? and supratemporal) to the articular condyle. The quadrate slopes sharply backward from the squamosal contact. These details can now only be seen in the cast, and not in the specimen.

In the palate (Text-fig. 3C), the premaxillae, maxillae and vomers cannot be seen in the specimen or in the cast, although Tatarinov (1978, p. 509) gave detailed description of all palatal elements. The palatines are difficult to distinguish, but appear to be elongate elements that contact the medial margins of the maxillae above the tooth rows, and are widely separated in the midline, with no evidence now of a midline contact. The right pterygoid shows the anterior and ectopterygoid processes and, in occlusal view, the deep quadrate process curving back to contact much of the medial face of the quadrate. There is no indication of a sphenethmoid, as identified by Tatarinov (1978, p. 510).

The braincase and epipterygoid are absent.

The reconstructed skull (Text-fig. 4) is based on the cast and on the specimen. The circumorbital and temporal regions were restored by moving cut-out bone shapes back to their original articulations. The top of the snout is crushed in both the cast and the specimen, and the nasal was lifted back to its original position. The anteriormost part of the snout, and the parietals, were based on *Prolacerta*.

Mandible. Both mandibular rami are present in the cast, but only the anterior half of the left ramus (Text-figs 3–4). In the specimen, the posterior part of the right ramus is now damaged, and the left ramus is missing. The mandible is narrow and shallow, exhibiting a sigmoid curve in ventral view. The dentary is a low straight element, which presumably bore teeth, but the dorsal margin is concealed within the skull. The splenial is essentially a medial element, but forms the ventral portion of the anterior part of the mandible, and extends some way up the lateral face of the left mandible in the cast. The splenial symphysis is missing. The sutures delimiting the angular, surangular, and prearticular are unclear. The articular and Meckel's canal cannot be seen, and it is not possible to determine whether there was a coronoid process.

Dentition. The right maxilla bears about 15 teeth (Text-fig. 3A, C), but when intervening gaps are included, the count may be 20–25. There are 13 or 14 teeth and gaps on the left maxilla. Dentary teeth cannot be seen. Tatarinov (1978, p. 510) indicated the presence of 'up to 40 teeth in the upper jaw, seven of which are in the premaxillary [and] about 35 teeth in the lower jaw', none of which can now be confirmed. The maxillary teeth are conical, slightly recurved, and have sharp points. They appear to be arranged with alternating teeth and gaps. The preservation of the specimen makes it difficult to determine whether the teeth sit in sockets; they appear to be surrounded by arcs of bone laterally, and to sit in a groove that is partially open on the medial side.

Tatarinov (1978, pp. 507, 510) described extensive midline rows of teeth on the vomer and pterygoid, but there is no evidence for teeth on any of the palatal elements.

Hyoid elements. A possible hyoid element is represented in the cast by a narrow rod-like bone (?hy, Text-fig. 3C), 5 mm long and 0·3 mm wide, below the right pterygoid, but is no longer visible in the fossil.

Axial skeleton. There are five cervical, nine dorsal and 29 caudal vertebrae, beautifully preserved, some of them still in articulation (Text-figs 5–8). The sacral vertebrae are absent.

The five cervicals appear to follow in sequence, but do not include either the atlas or axis. Hence, these five are probably presacrals 3–7 or 4–8, as suggested by Tatarinov (1978, p. 510). The anteriormost complete vertebra (3 or 4) is elongate and narrow (Text-fig. 6A–B), 7 mm long, with a constricted centrum that is arched high in the middle, and lacks a ventral keel. The articular faces of the centrum appear to be flat and sub-circular, the anterior being broader than the posterior. The neural canal is broad. There is a double rib attachment surface (diapophysis and parapophysis; da, pa, Text-fig. 6A–B) at the anterior margin of the centrum, clearly seen on the left. The zygapophyses project a short distance in front of, and behind, the
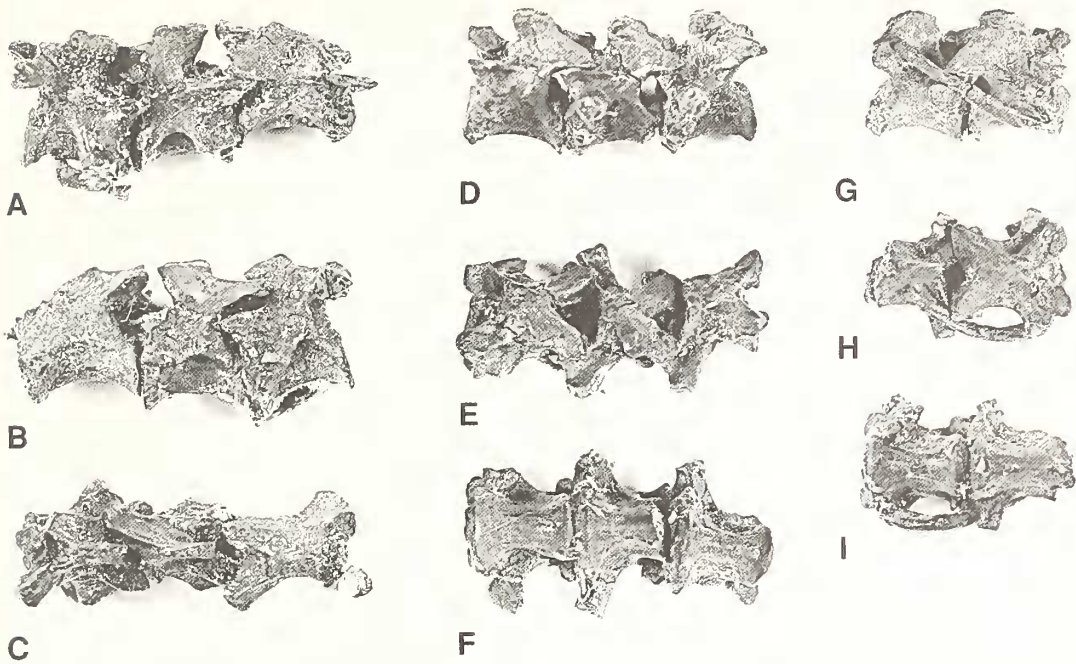
TEXT-FIG. 5. *Boreopricea funerea* Tatarinov, 1978. Vertebrae of PIN 3708/1. Cervical vertebrae 5 or 6 to 7 or 8, in right lateral (A), left lateral (B), and dorsal (C) views. Three anterior dorsal vertebrae, in left lateral (D), dorsal (E), and ventral (F) views. Two anterior dorsal vertebrae, with attached rib fragment, in left lateral (G), dorsal (H), and ventral (I) views. All × 2·5.
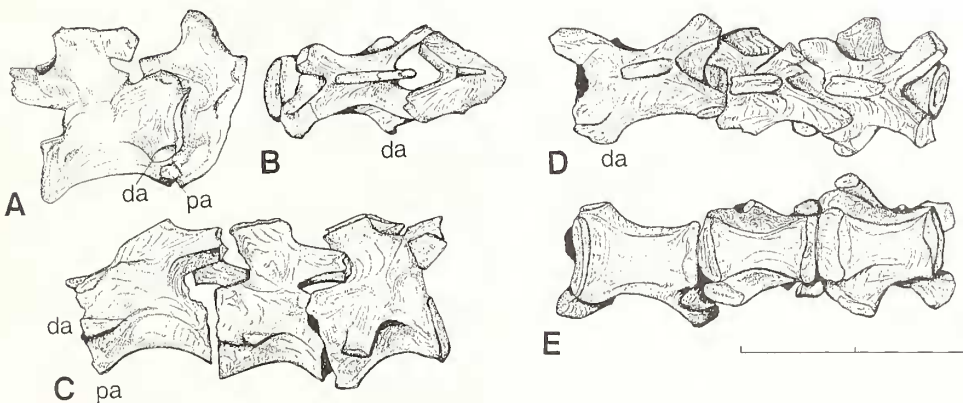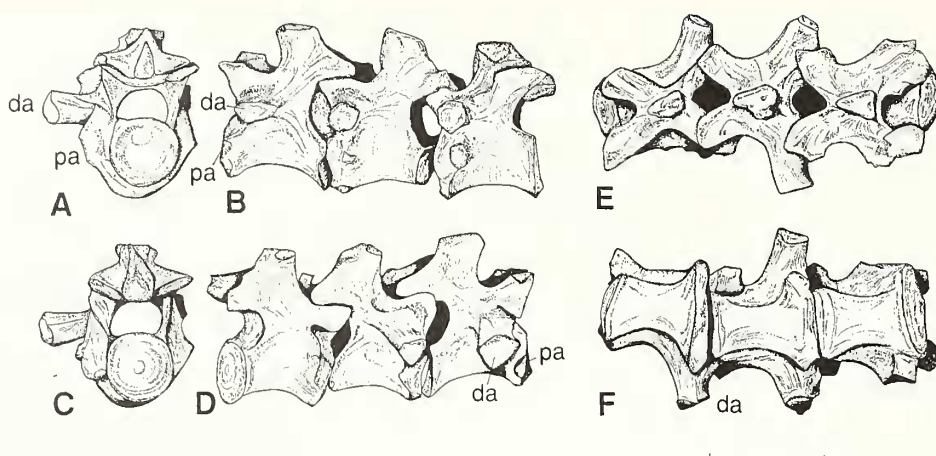

TEXT-FIG. 6. *Boreopricea funerea* Tatarinov, 1978. Cervical vertebrae of PIN 3708/1. Cervical vertebrae 3 and 4 or 4 and 5, in right lateral (A) and dorsal (B) views. Cervical vertebrae 5 or 6 to 7 or 8, in left lateral (C), dorsal (D), and ventral (E) views. Abbreviations: da, diapophysis; pa, parapophysis. Scale bar represents 10 mm.

centrum, and the zygapophyseal facets are angled at about 40° above horizontal. The neural spine is narrow, long (3·5 mm), and low, but the dorsal portion is apparently incomplete.

The three posterior cervical vertebrae 5/6–7/8 (Text-figs 5A–C, 6C–E) are slightly shorter, 5·5–6 mm long, and their centra are slightly broader than in the anterior cervicals. The rib attachment faces form a well-marked sub-triangular area on the anterior lateral margin of the centrum, with the parapophysis located somewhat ventrally, and the broader diapophysis projecting some distance laterally, especially in cervical 7/8 (da, pa,

TEXT-FIG. 7. *Boreopricea funerea* Tatarinov, 1978. Anterior dorsal vertebrae 5 or 6 to 7 or 8 of PIN 3708/1, in anterior (A), left lateral (B), posterior (C), right lateral (D), dorsal (E), and ventral (F) views. Abbreviations as for Text-figure 6. Scale bar represents 10 mm.
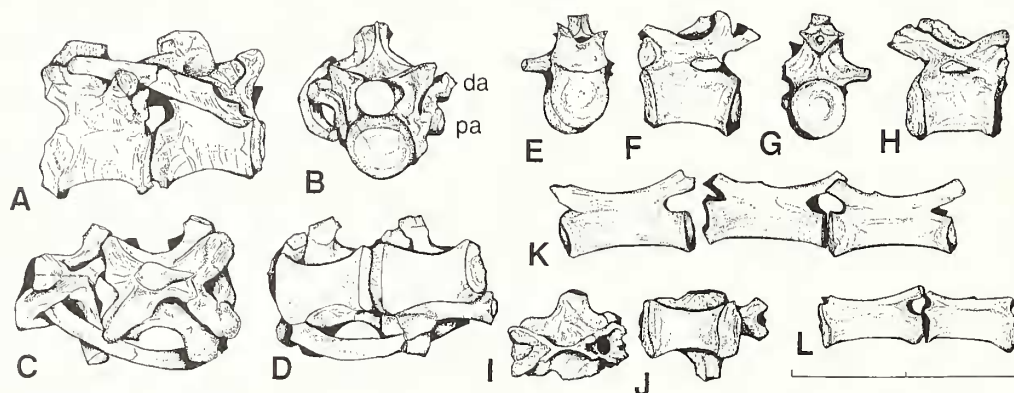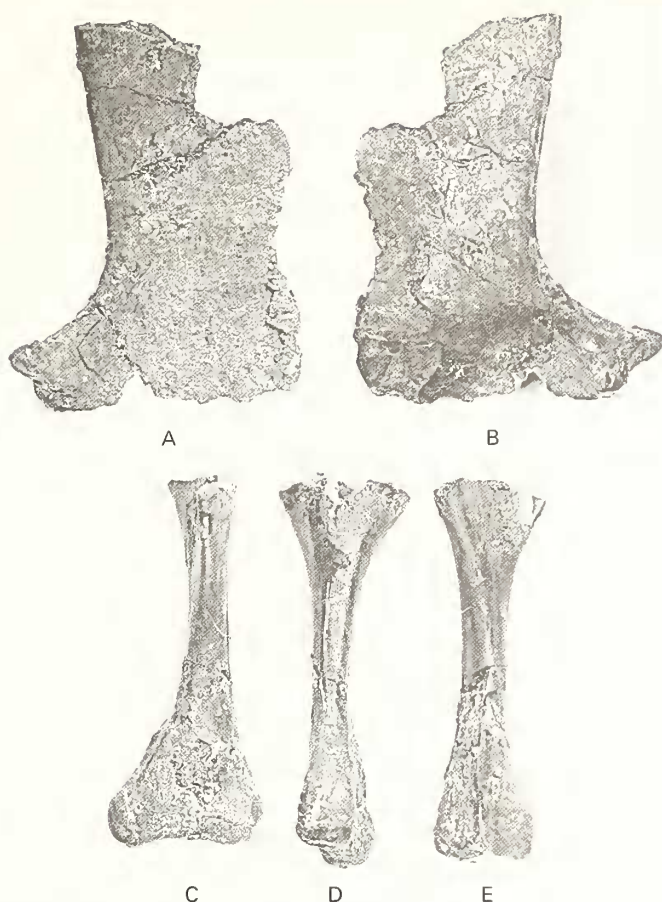

TEXT-FIG. 8. *Boreopricea funerea* Tatarinov, 1978. Dorsal and caudal vertebrae of PIN 3708/1. Anterior dorsal vertebrae, with attached rib fragment, in lateral (A), anterior (B), dorsal (C), and ventral (D) views. Anterior caudal vertebra 4 or 5, in anterior (E), left lateral (F), posterior (G), right lateral (H), dorsal (I), and ventral (J) views. K, mid-caudal vertebrae *c*. 19–21, in left lateral view. L, posterior caudal vertebrae *c*. 34–35, in left lateral view. Abbreviations as for Text-figure 6.

Text-fig. 6c–D). The zygapophyses spread more laterally than in cervical 3/4. The neural spines show a narrow dorsal spine table which is slightly expanded.

There are five well preserved anterior dorsal vertebrae, in a set of three and a set of two (Text-figs 5D–I, 7, 8A–D). Centra are shorter (5 mm) and broader than in the cervicals. The posterior articular face of the centrum is circular, but the broader anterior face is cordate to circular in outline. Both faces are amphicoelous. The centra are narrowly constricted and lack ventral keels. All show a small parapophyseal facet, now quite distinct from the laterally projecting transverse process (diapophysis) which had a sub-triangular lateral articular face (da, pa, Text-figs 7, 8B). The zygapophyses spread widely laterally, and their articular faces are set at an angle of only 20° above horizontal. The neural spines are short and low, and provided with a triangular spine table, with the tip of the triangle pointing back. A set of three poorly preserved posterior dorsal vertebrae show similar features, but no trace of a parapophysis.

There are 29 caudal vertebrae, each preserved whole or in part (Text-figs 2, 8E–L). These caudals are possibly 4–5, 7, 11–15, 16–22, 25–29, 30–32, 34–38, and 41, based upon their locations as glued on to the specimen card.

TEXT-FIG. 9. *Boreopricea funerea* Tatarinov, 1978. Scapula and humerus of PIN 3708/1. Right scapula, in lateral (A) and medial (B) views. Partial left humerus, lacking the proximal end, in anterior (C), dorsal (D), and ventral (E) views. All × 3·0.

The numbering, and narrowing of centra towards the more posterior elements, suggests that there were originally about 50 vertebrae in the tail.

The anterior caudals 4 and 5 (Text-fig. 8E–J) are short, with centra 4–4·5 mm long. The centrum is spool-shaped, but not as constricted as in presacral vertebrae, and the anterior and posterior articular faces are the same size. Distinct low transverse processes project horizontally. The neural spine and zygapophyses are incomplete. Caudal 7 (Text-fig. 2) is more complete, with a 4 mm long centrum. The vertebra shows a neural spine that slopes well back, and has a triangular spine table with an anterior point. The zygapophyses are small and articular faces are nearly horizontal. The anterior and posterior margins of the centrum have a broad rim, but there is no clear haemapophyseal facet. Tatarinov (1978, p. 511) reported a haemapophysis in contact with a caudal vertebra, but that bone is now lost. More posterior caudals (Text-fig. 8K–L) have slightly longer centra, 5–5·5 mm, but much lower and narrower. The neural spine blends with the postzygapophyses, and the transverse process disappears by caudal 16. The zygapophyseal facets become tiny.

A number of narrow rib shafts is preserved (Text-fig. 2), apparently associated with middle and posterior dorsal vertebrae, but the articular heads are not present. Some isolated rib heads are present with the specimen, but there is no evidence now for their correct assignment. Cervical, sacral and caudal ribs are now missing in the specimen.

Appendicular skeleton. Elements of the shoulder girdle, forelimbs and hindlimbs are preserved, but the pelvis is absent (Text-fig. 2). Some of the limbs bones in particular are remarkably well preserved, and it appears that
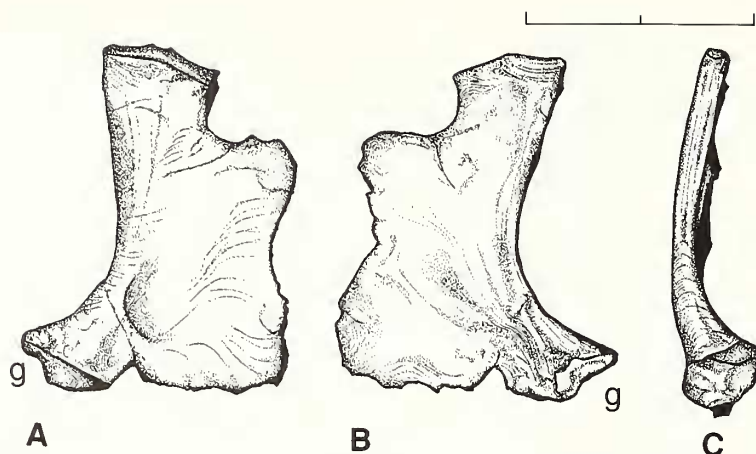
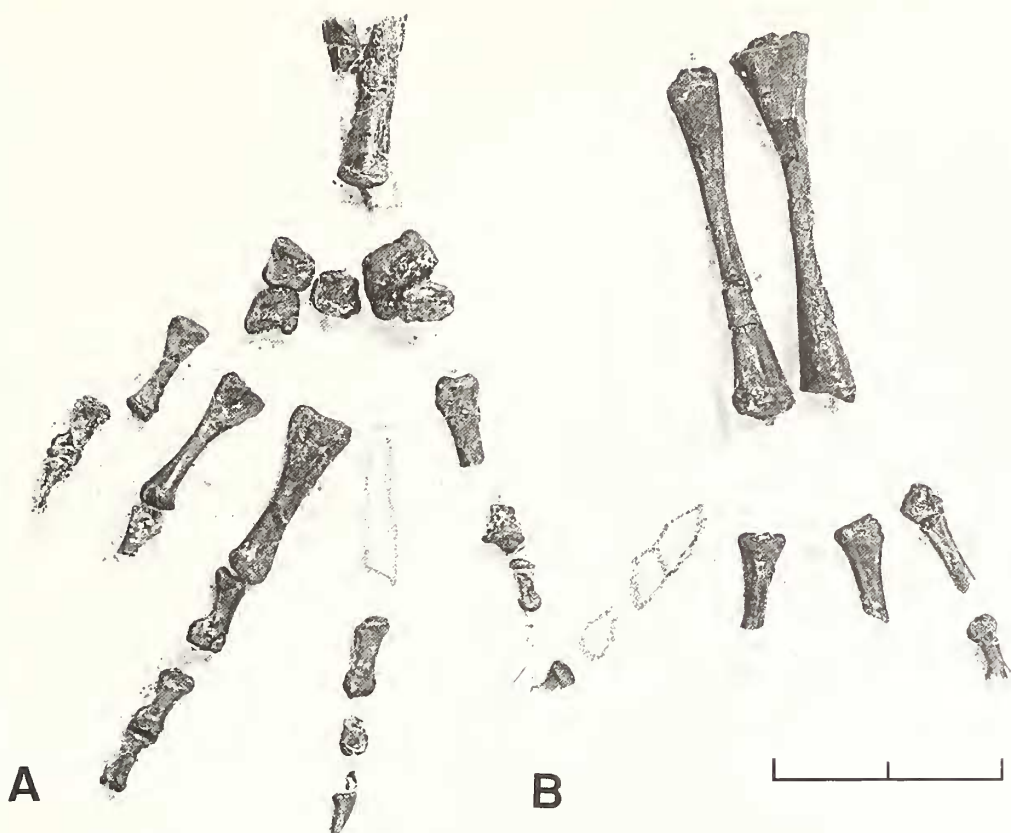TEXT-FIG. 10. *Boreopricea funerea* Tatarinov, 1978. Right scapula of PIN 3708/1, in lateral (A), medial (B), and posterior (C) views. Abbreviation: g, glenoid. Scale bar represents 10 mm.
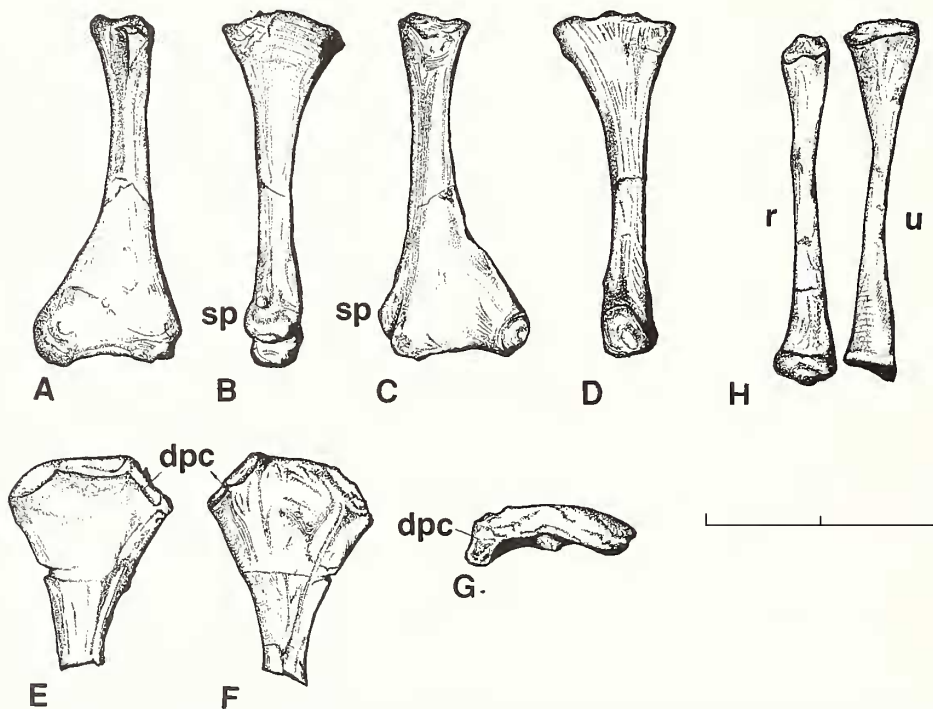
TEXT-FIG. 11. *Boreopricea funerea* Tatarinov, 1978. Forelimb elements of PIN 3708/1. Left humerus, lacking proximal end, in anterior (A), dorsal (B), posterior (C), and ventral (D) views. Proximal end of right humerus, in dorsal (E), ventral (F), and proximal (G) views. H, left radius (r) and ulna (u) in posterior view with proximal end at top. Abbreviation: dpc, deltopectoral crest; sp, supinator process. Scale bar represents 10 mm.

the hands and feet were complete, including every wrist and ankle bone, and every phalanx. Some of these elements are now missing. Tatarinov (1978, p. 511) described a clavicle, interclavicle, and an ossified sternum, but none of these elements can be located now.
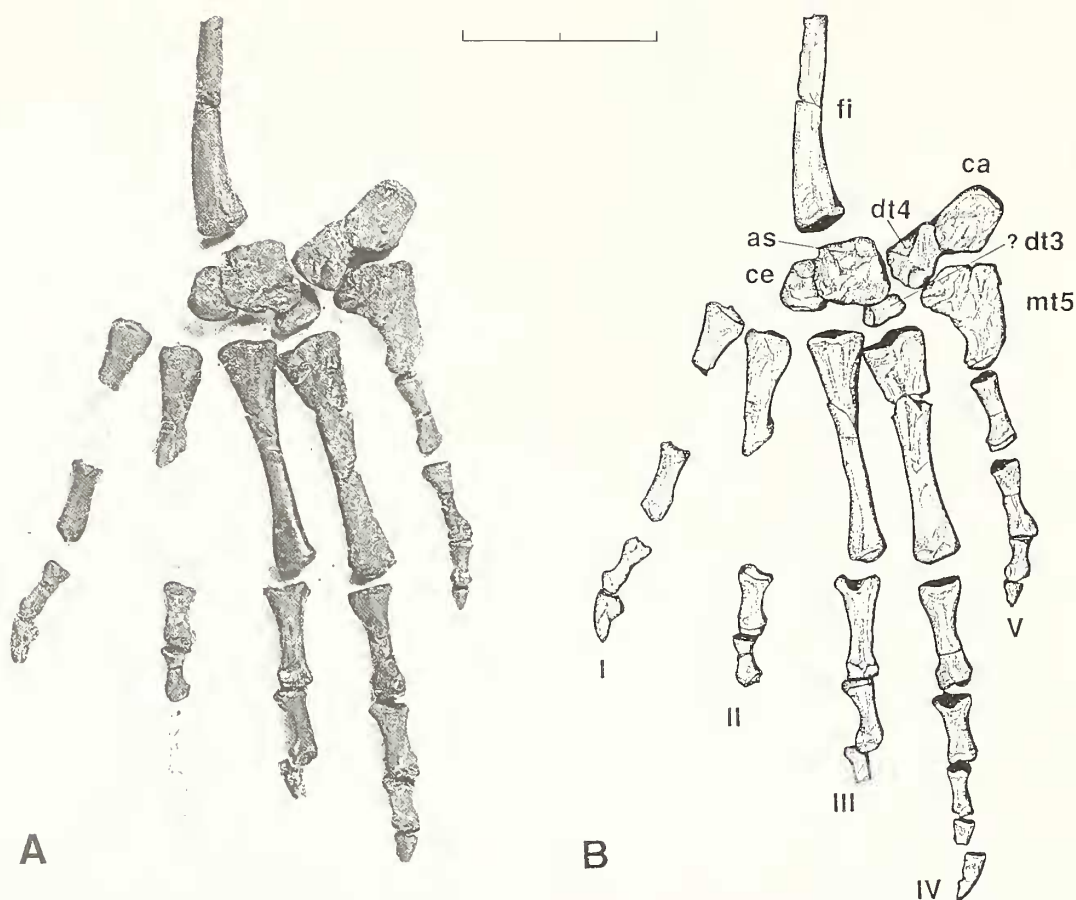
TEXT-FIG. 12. *Boreopricea funerea* Tatarinov, 1978. Right (A) and left (B) hands of PIN 3708/1, as stuck on the card. Individual elements are shown in a mixture of ventral and dorsal aspects. Pencil outlines indicate bones that are now missing. Scale bar represents 10 mm.

The two scapulae are broad elements, apparently quadratic in lateral view, but the thin dorsal and posterior margins are incomplete. The right scapula (Text-figs 9A–B, 10) is better preserved. It measures 16·5 mm high and 12·5 mm long. The whole scapular blade is thin, and it curves outwards, when seen in anterior view. The thicker anterior margin is deeply curved behind the broad glenoid. The articular face of the glenoid is triangular, with the point facing backwards (g, Text-fig. 10). The putative coracoid has a larger glenoid face, also triangular, and with the point facing backwards. Behind it, the bone is thin, and bears a small coracoid foramen. The thin ventral and posterior margins of the putative coracoid are incomplete.

The forelimb is represented (Text-fig. 2) by a nearly complete left humerus (shown as if the right-hand element, and with proximal and distal ends reversed, by Tatarinov 1978, fig. 2), the proximal end of the right humerus, the radius and ulna (complete on the left side only), and both hands (neither complete, but more so on the right side).

The nearly complete left humerus (Text-figs 9C–E, 11A–G), 17 mm long, has broad proximal and distal ends, set at right angles to each other. The distal end bears two condyles, for the radius and the ulna, separated by a constricted middle portion. There is a moderate supinator process (sp, Text-fig. 11B–C) with an ectepicondylar groove (not entepicondylar, as indicated by Tatarinov 1978, p. 511). There are no foramina. The shaft is approximately circular in cross section. The proximal end is more completely seen in the right humeral fragment (Text-fig. 11E–G), which shows a slender deltopectoral crest, projecting at an angle of about 100° from the proximal articular face (dpc, Text-fig. 11E–G). The ventral face of the proximal end of the right humerus is deeply concave, while the dorsal face is somewhat crushed. Comparison of the two incomplete humeri yields an original total length of 21 mm, with the proximal end (right side) 8 mm wide and the distal end (left side) 7 mm wide.
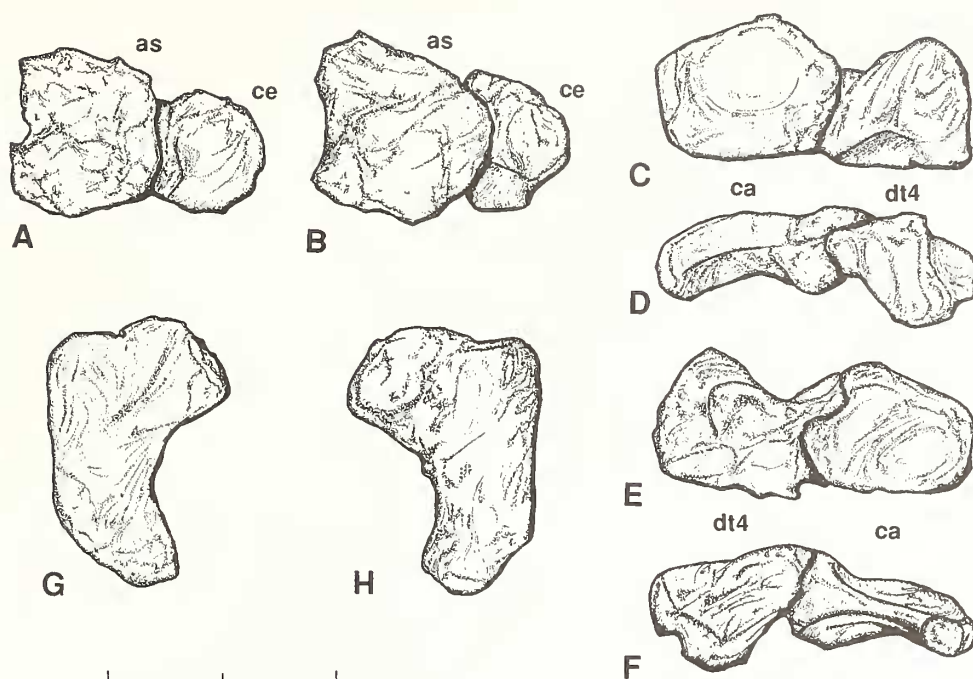
TEXT-FIG. 13. *Boreopricea funerea* Tatarinov, 1978. A–B, right foot, as stuck on the card, of PIN 3708/1, showing partial fibula, the four main tarsal bones, all five metatarsals, and most of the phalanges. Abbreviations: I, II, III, IV, V, digits 1, 2, 3, 4, and 5; as, astragalus; ca, calcaneum; ce, centrale; dt3, third distal tarsal; dt4, fourth distal tarsal; fi, fibula; mt5, metatarsal 5. Pencil outlines indicate bones that are now missing. Scale bar represents 10 mm.

The left ulna and radius (Text-figs 2, 11H) are 17 mm and 16·5 mm long respectively. Both elements are slightly curved rods with a narrow 1 mm wide shaft, and expanded flattened ends which overlap in natural articulation. The proximal end of the ulna (3·5 mm) is broader than the proximal end of the radius (2 mm), but the distal end of the ulna (2 mm) is narrower than the distal end of the radius (3 mm), as is usual in amniotes.

There are five small carpal elements in the wrist of the right hand (Text-fig. 12A), but these are too small and featureless for identification. The hands are secured on the card in ventral view, even though the rest of the skeleton is arrayed in dorsal view; hence digit 1 lies laterally and digit 5 is medial. Metacarpals 1–3 and 5 of the right hand, and 1, 2, and 4 of the left (Text-fig. 12B) indicate that metacarpal 3 was longest, and 2 was a little shorter. Eleven phalanges, including unguals on digits 1 and 4, are present in the right hand, and ten phalanges in the left, including unguals on digits 1 and 5. It is not clear whether all the elements are now in their correct positions, and a phalangeal formula cannot be given.

Two femora are preserved (Text-fig. 2), a partial right lacking the distal end, and a nearly complete left, 25 mm long. The bone appears to be hollow, the left femur showing a calcite core in a broken area of the shaft. The distal end of the left femur is broader (5·5 mm) than the proximal (4 mm). The proximal end shows a sub-

TEXT-FIG. 14. *Boreopricea funerea* Tatarinov, 1978. Elements of the tarsus of the right foot of PIN 3708/1. Astragalus and centrale in close apposition, in dorsal (A) and ventral (B) views. Calcaneum and distal tarsal 4 in close apposition, in dorsal (C), distal (D), ventral (E), and proximal (F) views. Metatarsal 5 in dorsal (G) and ventral (H) views. Abbreviations as for Text-figure 13. Scale bar represents 5 mm.

circular articular face, while the distal end is probably more elliptical in outline. The shaft of the left femur shows a slight sigmoid bend, when viewed from above or below.

The lower hindlimb is represented by most of the left tibia, the distal end of the right fibula, and a proximal fragment of the left fibula (Text-fig. 2). The tibia has a broad sub-triangular proximal end, 5 mm wide, and a low cnemial crest. The specimen is 17 mm long, and shows the beginnings of a distal expansion, so it may have been about 20 mm long when complete. The fibula is a slender flat element, 2×1 mm proximally and 3×2.5 mm distally. The right fibula shows a clear curve in the shaft.

The foot is preserved incompletely on the left, but is nearly complete on the right (Text-figs 13–15), and the description is based entirely on the latter. The foot is glued in ventral view on the card, and digit 1 lies laterally, digit 5 medially, but individual elements are secured variously in dorsal and ventral views. The proximal part of the ankle appears to consist of four elements arranged in two pairs, a centrale and astragalus (= intermedium) and a distal tarsal 4 and calcaneum (= fibulare). In both cases, the elements fit tightly together and cannot be separated, but lines of contact are still visible.

The centrale is a hemispherical element with a concave lateral facet that fits snugly over the medial margin of the astragalus (Text-figs 13, 14A–B). The astragalus is a larger quadratic element that bears two distal articular surfaces, one for the calcaneum, and one for distal tarsal 4. The articulation with the calcaneum may have been more extensive than shown in Text-figure 15, since part of the lateral margin of the astragalus is broken off. The centrale bears a proximal articular face for the tibia, whilst the astragalus contributes to this tibial contact, as well as meeting the fibula.

The calcaneum (Text-figs 13, 14C–F) is of equal depth to the astragalus at the point of articulation. There does not seem to be a foramen between astragalus and calcaneum. The lateral tuber (lt, Text-fig. 15) is 3.5 mm long, almost rectangular, and curves slightly upwards. Both dorsal and ventral surfaces of the tuber are smooth and slightly concave. The calcaneum articulates with distal tarsal 4, although the nature of this articulation is obscured by their firm connection. Distal tarsal 4 shows two distal articular facets (Text-fig. 14D), one sub-rectangular and the other sub-triangular, the former for contact with metatarsal 5. It is not clear how the latter
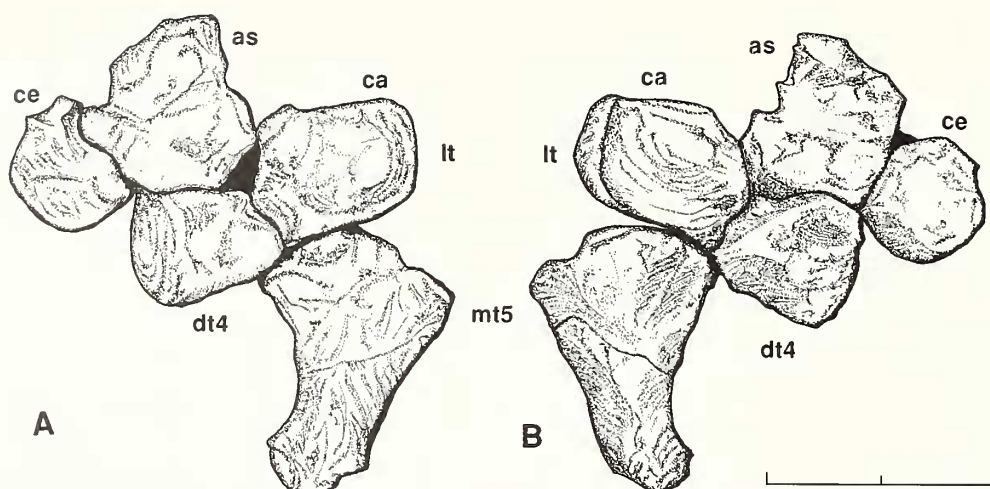
TEXT-FIG. 15. *Boreopricea funerea* Tatarinov, 1978. Reconstructed tarsus of the right foot of PIN 3708/1 in ventral (A) and dorsal (B) views, showing the likely pattern of fit of the four main proximal tarsal elements and metatarsal 5. Abbreviations as for Text-figure 13; lt, lateral tuber. Scale bar represents 5 mm.

facet articulated with the other ankle bones, since the full series of distal tarsals is unknown. A small bean-shaped distal element is present, probably distal tarsal 3.

The approximate equivalence in size of the astragalus, calcaneum, centrale, and distal tarsal 4 is a feature shared with *Prolacerta* (Gow 1975) and *Macrocnemus* (Rieppel 1989), and the particular arrangement of these four elements, including the contact of centrale and tibia, may turn out to be a prolacertiform synapomorphy. It is not included here in the cladistic analysis until a more detailed study of other prolacertiform specimens can be carried out.

The hooked fifth metatarsal (Text-figs 13, 14G–H), 6·5 mm long, bears an ovoid proximal articular surface with a sharp edge ventrally and a rounded facet dorsally. This surface articulates with distal tarsal 4 and the calcaneum. The dorsal rounded articulation of metatarsal 5 may have allowed this element to bend up more than down. Distally, the fifth metatarsal narrows and is bounded by a straight lateral margin and a hooked medial margin.

Most of the other toe bones are present. Metatarsals 1 and 2 are incomplete distally, 3 to 5 are complete. Metatarsals 3 and 4 are slender elements, 12·5 mm and 13·0 mm long, with flattened expanded proximal and distal ends and a shaft that arches dorsally. Metatarsal 4 is longest, then 3, then perhaps 2, 1, and 5 in order of diminishing length. Sixteen phalanges are present, and these include small pointed unguals on digits 1, 4 and 5. The phalanges have been stuck on card rather inaccurately, since they indicate the unlikely phalangeal formula of 3-3-3/4-4-4. Tatarinov (1978, p. 511) indicated a more typical reptilian phalangeal formula of 2-3-4-5-4 (illustrated as 2-3-4-5-5 in his Text-fig. 2).

RELATIONSHIPS AMONG PROLACERTIFORMS

Previous work

Until recently, the prolacertiforms were of uncertain affinities. Some, or all, taxa were assigned by Romer (1966) to Euryapsida, as basal relatives of the plesiosaurs and ichthyosaurs. Other authors regarded the prolacertiforms, as their name implies, as 'pre-lizards' on the basis of a variety of shared characters, summarized by Wild (1973, 1980). An affinity with archosaurs was hinted at by Cruickshank (1972), and Gow (1975) explicitly noted the close relationship of *Prolacerta* with archosaurs. Benton (1983, 1984, 1985) listed synapomorphies of prolacertiforms and archosaurs, and he suggested that their closest outgroups are Rhynchosauria and *Trilophosaurus*, the whole forming a clade termed the Archosauromorpha (von Huene 1946). Evans (1988) confirmed this view, and added *Megalancosaurus*, Thalattosauria, Kuehneosauridae (tentatively), and Choristo-

TABLE 1. The species of prolacertiforms, arranged in stratigraphical sequence. Main descriptive accounts for each taxon are noted.

Late Permian (Kazanian):
 Protorosaurus speneri Meyer, 1856; Kupferschiefer, Germany (Seeley 1888).
Early Triassic (Scythian):
 Boreopricea funerea Tatarinov, 1978; Vetluzhian Series, Kolguyev Island,
   Russia (Tatarinov 1978).
 Kadimakara australiensis Bartholomai, 1979; Rewan Formation,
   Queensland, Australia (Bartholomai 1979).
 Prolacerta broomi Parrington, 1935; *Lystrosaurus* Zone, South Africa (Gow
   1975; Evans 1986); Fremouw Formation, Antarctica (Colbert 1987).
 Prolacertoides jimusarensis Young, 1973; Xinjiang, China (Young 1973).
 Trachelosaurus fischeri Broili and Fischer, 1916; Buntsandstein, Germany
   (Broili and Fischer 1916).
Mid Triassic (Anisian):
 Tanystropheus antiquus von Huene, 1905; Oberer Buntsandstein, Unterer
   Muschelkalk, Germany (Ortlam 1967; Wild 1973); Gogolin Beds, Poland;
   Unterer Muschelkalk, Netherlands (Wild and Oosterink 1984).
 Rhombopholis scutulata (Owen, 1842); Bromsgrove Sandstone Formation,
   Warwick and Bromsgrove, England (Benton and Walker 1996).
Middle Triassic (Ladinian, or Anisian/Ladinian boundary):
 Cosesaurus aviceps Ellenberger and Villalta, 1976; Montral-Alcover,
   Tarragona, Spain (Ellenberger 1977; Sanz and Lopez-Martinez 1984).
 Macrocnemus bassanii (Nopcsa, 1930); Grenzbitumenzone, Switzerland
   and Italy (Peyer 1937; Kuhn-Schnyder 1962; Rieppel 1989).
 Tanystropheus longobardicus (Bassani, 1886); Grenzbitumenzone,
   Switzerland and Italy (Wild 1973, 1980).
 Tanystropheus conspicuus Meyer, 1855; Oberer Muschelkalk and
   Lettenkeuper, Germany (Wild 1973, 1980) [? = *T. longobardicus*].
 Tanystropheus meridensis Wild, 1980; Meridekalk (Lettenkeuper),
   Switzerland (Wild 1980).
Late Triassic (Carnian):
 Malerisaurus langstoni Chatterjee, 1986; Tecovas Member, Dockum
   Formation, Texas, USA (Chatterjee 1986).
 Malerisaurus robinsonae Chatterjee, 1980; Maleri Formation, India
   (Chatterjee 1980).
 Tanytrachelos ahynis Olsen, 1979; Dan River Group, North Carolina and
   Virginia, USA (Olsen 1979).
Late Triassic (Norian):
 Langobardisaurus pandolfi Renesto, 1994; Calcare di Zorzino, Cene,
   northern Italy (Renesto 1994*a*).
 Megalancosaurus preonensis Calzavara, Muscio and Wild, 1980; Calcare di
   Zorzino, Cene, northern Italy (Renesto 1994*b*).
 Tanystropheus fossai Wild, 1980; Argillite di Riva di Solto, northern Italy
   (Wild 1980).

dera to the clade. Recent analyses have confirmed this pattern (e.g. Chatterjee 1986; Rieppel 1989; Laurin 1991; Renesto 1991, 1994*a*, 1994*b*).

Relationships within the clade Prolacertiformes have proved harder to establish. The Late Permian *Protorosaurus* has generally been indicated as the most plesiomorphic member of the group (Benton 1985; Evans 1988), and the Mid and Late Triassic *Tanystropheus* and the Late Triassic *Tanytrachelos* have been paired as sister-taxa. However, the Mid Triassic *Macrocnemus* has shuttled between close alliance with the Early Triassic *Prolacerta* and *Tanystropheus*, while the position of

TABLE 2. Characters used in the assessment of the phylogenetic relationships of the prolacertiforms. Some of these characters were proposed by Benton (1985) and Evans (1988). The postulated plesiomorphic (0) and apomorphic/derived (1) states of each character are noted.

Skull characters:
1. Dorsomedial process of premaxilla: extends between narial openings (0); reduced (1).
2. Relative length of nasals and frontals: nasals shorter than frontals (0); nasals longer than frontals (1).
3. Fronto-parietal suture: interdigitating (0); straight (1).
4. Pineal foramen: present and relatively large (0); reduced or absent (1).
5. Lacrimal contact with nasal: present (0); absent (1).
6. Lacrimal extent: element runs forward from the orbit (0); restricted to the orbital rim in lateral view (1).
7. Postfrontal dimensions: substantial tripartite element (0); short element lacking clear processes (1).
8. Posterior process of postorbital: does not extend beyond back of lower temporal fenestra (0); extends back beyond the posterior margin of the lower temporal fenestra (1).
9. Ventral ramus of squamosal: present, and extends below quadrate head (0); reduced and cotyle formed for quadrate head (1).
10. Posterior process of jugal: present (0); absent (1).
11. Quadratojugal shape; an indicator of whether there is a complete lower temporal bar: low and with anterior process (0); tall with reduced anterior process (1).
12. Quadratojugal: present (0); absent (1).
13. Supratemporal: present (0); absent (1).
14. Relative positions of posterior terminations of tooth rows: posterior dentary teeth lie level with, or behind, posterior maxillary teeth (0); posterior dentary teeth lie anterior to posterior maxillary teeth (1).
15. Numbers of premaxillary teeth on each side: seven or fewer (0); more than seven (1).
16. Pterygoid flange teeth; present (0); absent (1).

Postcranial characters:
17. Numbers of cervical vertebrae: seven or fewer (0); more than seven (1).
18. Numbers of cervical vertebrae: fewer than ten (0); ten or more (1).
19. Relative lengths of mid and posterior cervical and dorsal vertebral centra: cervical centra subequal in length to dorsals (0); cervical centra longer than dorsals (1).
20. Cervical neural spine shape: short and tall (0); long and low (1).
21. Ovoid spine-table on top of neural spine: absent (0); present (1).
22. Cervical ribs: short and stout (0); long and slender (1).
23. Neural spines of dorsal vertebrae: short and slender (0); tall and rectangular (1).
24. Trunk intercentra: present (0); absent (1).
25. Attachment of ribs to posterior dorsal vertebrae: not fused (0); fused (1).
26. Scapula shape: tall, and larger than coracoid (0); low, and subequal in size to coracoid (1).
27. Entepicondylar groove or foramen in humerus: present (0); absent (1).
28. Radius length relative to humerus: radius 80–90 per cent. length of humerus (0); radius 40–65 per cent. length of humerus (1).
29. Intermedium in carpus: present (0); absent (1).
30. Centralia in the manus: present (0); absent (1).
31. First distal carpal: present (0); absent (1).
32. Relative lengths of metacarpals 3 and 4: metacarpal 3 shorter than 4 (0); metacarpal 3 equal in length to, or longer than, 4 (1).
33. Relative lengths of metacarpals 1 and 5: shorter than metacarpals 2 and 4 (0); similar in length to metacarpals 2 and 4 (1).
34. Ilium length relative to ischium: longer (0); equal or shorter (1).
35. Preacetabular buttress on ilium: absent, or insignificant (0); well-developed (1).
36. Thyroid foramen in the pelvis: absent (0); present (1).

TABLE 2. *(cont.)*

---

37. Pubis shape: broad (0); narrow and waisted (1).
38. Femur shape: sigmoidal (0); straight (1).
39. Length of tibia relative to length of femur: tibia shorter than, or subequal to, femur in length (0); tibia longer than femur (1).
40. Foramen in ankle between astragalus and calcaneum: present (0); absent (1).
41. Lateral calcaneal tuber: absent (0); present (1).
42. Pes centrale: present (0); absent (1).
43. First distal tarsal: present (0); absent (1).
44. Second distal tarsal: present (0); absent (1).
45. Relative lengths of metatarsals 4 and 5: metatarsal 4 less than three times length of metatarsal 5 (0); metatarsal 4 more than three times length of metatarsal 5 (1).
46. Metatarsal 5 shape: L-shaped (0); symmetrical and very short (1).
47. Relative length of second phalanx on digit 5 of foot: short (0); long (1).
48. Postcloacal bones: absent (0); present (1).

Malerisaurus has been unclear. Other less well known taxa have been even harder to place. Apart from the practical problems of study of many of these taxa (see below), there seems to be rampant homoplasy within the group.

Materials and methods used in the analysis

Nineteen species of prolacertiforms, in 14 genera, have been described, and these range in age from Late Permian to Late Triassic (Table 1). The material upon which each of these taxa has been established is highly variable, some (e.g. *Protorosaurus*, *Prolacerta*, *Macrocnemus*, *Tanystropheus longobardicus*, *Malerisaurus robinsonae*, *Tanytrachelos*, *Megalancosaurus*) being founded on extensive and relatively complete skeletons, whilst the others are known from less substantial material. The least well known of the listed taxa are *Prolacertoides*, *Tanystropheus antiquus*, *T. fossai* and *Rhombopholis*. The preservation of *Macrocnemus*, *T. longobardicus* and *Tanytrachelos* as compressed fossils makes character determination difficult. The assignment of Mid and Late Triassic material from the Germanic Basin to species of *Macrocnemus* and *Tanystropheus* has also been problematical. In particular, most specimens assigned to *T. antiquus* and *T. conspicuus* are isolated, and there is often little evidence for affinities other than geological age. Wild (1980) may be right in suggesting that *T. conspicuus* is synonymous with *T. longobardicus*, and that *T. antiquus* may belong to another genus.

For the present cladistic analysis, 48 characters that vary among the prolacertiform taxa (Table 2) were tested. Polarities of characters were determined by reference to close outgroups, and three genera were chosen as outgroup taxa for the analyses, namely *Youngina* (Gow 1975), *Rhynchosaurus* (Benton 1990), and *Trilophosaurus* (Gregory 1945). These three taxa were chosen to include a close outgroup of Archosauromorpha (*Youngina*), and two non-prolacertiform archosauromorphs (*Rhynchosaurus*, *Trilophosaurus*). Each is plesiomorphic within its group, and each has been described in some detail. None of these three showed the plesiomorphic state for all characters.

Many of the characters used in previous cladistic analyses of diapsid relationships proved to be ill-defined, hard to code, or redundant. Nonetheless, many of the remaining characters are not entirely satisfactory, falling into a variety of categories: (1) characters based on relative lengths, which could be size-dependent in part (characters 2, 19, 26, 28, 32–34, 39, 45); (2) characters based on absence (?losses) of features, which could have arisen several times independently (characters 10–13, 16); (3) characters based on presences and absences of wrist and ankle bones, which may be prone to individual variation in patterns of ossification (Rieppel 1989), and indeed may be heavily subject to the vagaries of preservation (characters 29–31, 40–44). Despite these problems, it would be wrong to reject all such characters as suspect; it is better simply to regard them as provisionally

TABLE 3. Matrix of binary character-state codes for prolacertiforms. The taxa are listed in Table 1, and the characters in Table 2. Uncertain and unpreserved states are given as '?', and inapplicable characters as 'N'.

|	Skull characters				Postcranial characters					
	1	5	10	15	21	26	31	36	41	46
Youngina	01000	00100	00010	0	00000	00000	00000	00110	00000	00000 00
Rhynchosaurus	00001	00000	00000	0	00000	00100	00001	10100	01000	00000 00
Trilophosaurus	0001?	?0000	???00	1	00000	01000	01000	00010	00001	00000 00
Megalancosaurus	?????	????0	????0	?	00110	?1?10	1100?	1101?	01001	00001 1?
Protorosaurus	?100?	0?0??	?????	0	10110	11000	00000	?11?0	00001	00010 ?0
Boreopricea	?01?0	00001	1001?	?	1011?	?1?00	00???	10???	?0011	0??00 1?
Kadimakara	??000	00010	1001?	?	?????	?????	?????	?????	?????	????? ??
Prolacerta	11000	00001	10010	0	10111	11000	00000	00010	00101	00000 00
Prolacertoides	?1??0	0????	?????	1	?????	?????	?????	?????	?????	????? ??
Trachelosaurus	?????	????0	????0	?	11111	1110?	?????	???1?	?0???	????? ??
Tanystropheus antiquus	?????	?????	?????	?	10111	11???	?????	?????	?????	????? ??
Rhombopholis	?????	?????	?????	?	??11	11???	?????	???1?	?0???	????? ??
Cosesaurus	?????	???10	10?01	?	1011?	11101	?0???	100??	00010	01111 1?
Macrocnemus	0?001	00001	10001	0	10111	11101	10000	00011	10100	00110 ?0
Tanystropheus longobardicus	11101	11010	11000	0	11111	11?11	00111	10101	10000	11111 11
Tanystropheus meridensis	00000	01010	N10?0	0	??11?	1????	?????	?????	?????	????? ??
Malerisaurus langstoni	??0?	????0	?????	?	1011?	?1100	00???	??010	000??	????? ??
Malerisaurus robinsonae	00010	11000	00100	0	10111	?1100	00???	??010	00011	11100 ??
Tanytrachelos	01010	11110	??00	1	11111	11111	11???	1111?	1010?	11111 11
Tanystropheus fossai	?????	?????	?????	?	??1?	1????	?????	?????	?????	????? ??
Langobardisaurus	0????	?????	???0	?	10110	10?11	100??	00??1	10010	0??10 0?

phylogenetically informative, and to look for further systematic work on prolacertiform anatomy to reveal further details.

All prolacertiform taxa were coded, as far as possible, yielding a character-state data matrix (Table 3). The high proportion of missing data is evident, and this suggests that a search for the most parsimonious tree (MPT) would be unlikely to produce a valid result (Smith 1993; Swofford 1993). The data were analysed by PAUP (version 3.1.1; Swofford 1993), using the exact branch-and-bound algorithm that is guaranteed to find all MPTs. Where more than one MPT was produced, consensus trees were obtained by the strict and Adams techniques.

The missing data are unevenly spread in the matrix (Table 3), with some taxa being complete enough that all, or nearly all, characters could be coded, whilst others, such as *Prolacertoides*, *Tanystropheus antiquus*, *Rhombopholis* and *T. fossai*, exhibited fewer than 10 per cent. of characters. There are two approaches for dealing with large quantities of missing data. One is to cull poorly coded taxa, as was done for example by Fraser and Benton (1989), on the basis that cladistic analyses based on high quantities of missing data are likely to produce poorly resolved, or spurious, phylogenetic trees, and the analytical runs may last for immense amounts of time. The problem with this approach, as pointed out by Wilkinson (1992), is that it makes no distinction between characters that offer useful phylogenetic information and those that do not. Certain characters may be crucial in identifying the position of a taxon with respect to a particular node in the cladogram, and even very poorly coded taxa may reveal such characters. An example is *Prolacertoides*, which has only 8 per cent. of states coded, but the four codable states together cannot be matched with any other taxon.

The second approach, used here, is to apply 'safe deletion rules' (Wilkinson 1992; Wilkinson and
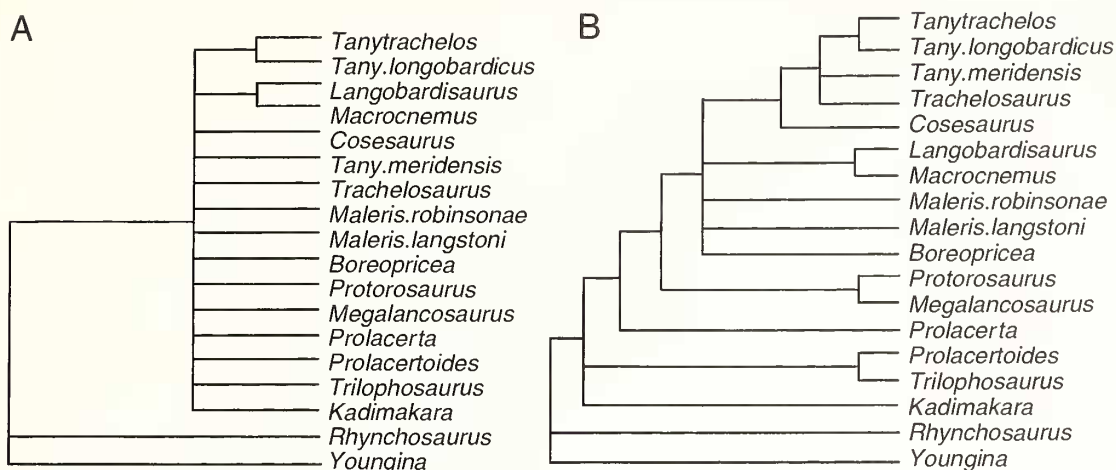
TEXT-FIG. 16. Cladograms showing the relationships of prolacertiforms, based on an analysis of the data matrix in Table 3, using the exact branch-and-bound technique in PAUP 3.1.1. *Youngina*, *Rhynchosaurus* and *Trilophosaurus* are outgroups. Redundant taxa (*Tanystropheus antiquus*, *T. fossai*, *Rhombopholis*) are omitted (see text). Strict (A) and Adams (B) consensus trees of the 450 MPTs. Tree statistics: length, 95; consistency index, 0·474; homoplasy index, 0·526; retention index, 0·561; rescaled consistency index, 0·266.

Benton 1996) that remove redundant information, but retain all phylogenetically informative entries. The sequence of deletions is as follows:

1. Remove all autapomorphies of individual species: there were three of these (characters 13, 29–30).
2. Remove all taxa that contribute nothing to the analysis since they are identical in every known respect to another more substantially coded taxon. Three poorly coded taxa, *Tanystropheus antiquus*, *T. fossai* and *Rhombopholis*, were deleted at this point since the first is identical in coded sites to *Macrocnemus* and other taxa, and the last two are identical, so far as one can tell, to *Prolacerta*, *Macrocnemus* and *Malerisaurus robinsonae*.

Wilkinson (1994) noted that the consensus trees commonly produced by PAUP are unsatisfactory. The strict consensus method is insensitive since it includes only those branching points that are found in all MPTs, and excludes all others, even those that are found in a majority of cases. The Adams consensus method is ambiguous since it includes all nestings that are common to all MPTs, but the topology of the consensus tree does not occur in all MPTs. Hence, Wilkinson (1994) proposed a Reduced Adams Consensus (RAC) method, in which the ambiguity of matching the Adams consensus tree to the MPTs from which it was constructed is obviated. The RAC technique involves selective pruning of taxa that contribute to polytomies until those polytomies disappear. Taxa were pruned according to the rules given by Wilkinson (1994) until a single fully-resolved RAC was obtained, but with the proviso of deleting as few taxa as possible.

Results

The first analysis, with autapomorphies (characters 13, 29–30) and redundant taxa (*Tanystropheus antiquus*, *T. fossai*, *Rhombopholis*) deleted, yielded many MPTs. The strict consensus tree (Text-fig. 16A) shows pairings of *Macrocnemus + Langobardisaurus* and *Tanystropheus longobardicus + Tanytrachelos*, whilst all other prolacertiforms form an unresolved polytomy with *Trilophosaurus*, a supposed outgroup taxon. *Youngina* and *Rhynchosaurus*, the other two outgroup taxa, form an unresolved trichotomy with the prolacertiform clade.

The Adams consensus trees (Text-fig. 16B) shows the pairings just noted, but is resolved further, with pairings of *Trilophosaurus + Prolacertoides*, and *Megalancosaurus + Protorosaurus*. The Adams tree also shows a tanystropheid clade, consisting of species of *Tanystropheus* and *Tanytrachelos*,
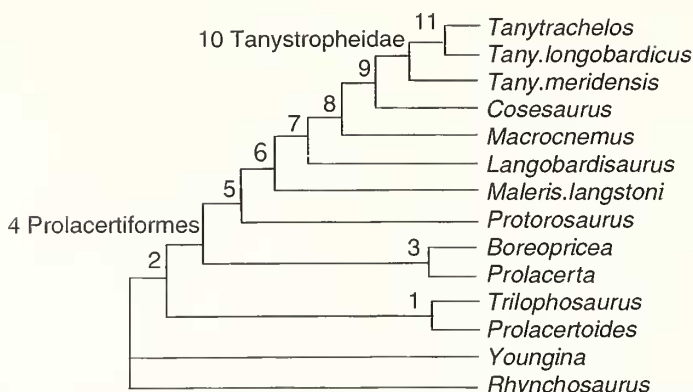
TEXT-FIG. 17. Reduced Adams Consensus tree produced according to the methods of Wilkinson (1994), by manipulation of the taxa that contribute to polytomies in the original Adams consensus tree (Text-fig. 16B). Additional deleted taxa were *Kadimakara*, *Megalancosaurus*, *Malerisaurus robinsoni* and *Trachelosaurus*. Tree statistics: length, 78; consistency index, 0·577; homoplasy index, 0·423; retention index, 0·629; rescaled consistency index, 0·363. Nodes are numbered, and clade names given for nodes 4 and 10 (see text). Bootstrap values (for 1000 replicates) were less than 50 per cent. for all nodes except 2 (72 per cent.) and 11 (68 per cent.).

with *Trachelosaurus* possibly associated. This clade is nested in a larger clade which includes *Cosesaurus*, *Macrocnemus*, *Langobardisaurus*, *Malerisaurus* and *Boreopricea*.

The Adams consensus tree (Text-fig. 16B) was incompletely resolved, so taxa contributing to the four polytomies were deleted to produce a single fully resolved RAC. The deleted taxa were *Megalancosaurus*, *Kadimakara*, *Trachelosaurus* and *Malerisaurus robinsoni*. The last three taxa contributed to three of the polytomies, and their deletion resolved those nodes. After these deletions, *Megalancosaurus* shifted into a tetratomy with *Protorosaurus*, *Boreopricea + Prolacerta*, and a clade of the six tanystropheids and *Macrocnemus*. Deletion of *Megalancosaurus* dissolved that tetratomy, and yielded a single MPT (Text-fig. 17). These procedures produce a RAC tree exhibiting the three properties identified by Wilkinson (1994) as essential: unambiguity, nonredundancy and informativeness.

In the fully resolved cladogram of prolacertiform relationships, the enigmatic *Prolacertoides* appears as the sister group of the outgroup taxon *Trilophosaurus*, as discovered by Evans (1988). *Boreopricea* and *Prolacerta* pair as sister groups and they appear next in the cladogram. The group Prolacertiformes is defined here as *Boreopricea + Prolacerta* and *Tanytrachelos*, and all taxa included in the cladogram (Text-fig. 17) between these three. *Protorosaurus* does not appear as the basal prolacertiform. This is surprising since it predates all other members of the clade by at least 10 My, and initial cladistic studies (Benton 1985) suggested that it was the most plesiomorphic form. However, slight variants of the cladogram, for example with *Malerisaurus langstoni* deleted instead of *M. robinsonae*, show *Protorosaurus* as the basal prolacertiform. This confirms Evans' (1988) finding of an unresolved position for this taxon. In the presence of the deleted taxa, *Protorosaurus* is apparently a sister group of the unusual *Megalancosaurus*, and those two appear in a more derived position in the cladogram (Text-fig. 16B) than *Prolacerta*.

The Triassic prolacertiforms are outgroups to the tanystropheid clade (Text-fig. 17). There is no evidence for the pairing of *Prolacerta* and *Macrocnemus* suggested by Benton (1985) and others. The present study does not permit clear division of the Prolacertiformes into subgroups, although a family Tanystropheidae, consisting of the species *Tanystropheus longobardicus* and *T. meridensis*, and *Tanytrachelos*, but excluding '*T.*' *antiquus*, may be recognized. *Boreopricea* here is a basal prolacertiform, but in other solutions, for example with *Malerisaurus langstoni* instead of *M. robinsonae* deleted, *Boreopricea* forms part of the macrocnemid/malerisaurid/tanystropheid clade, an assemblage of generally younger forms, as suggested by Evans (1988).

This cladogram is not uniformly stable. Only two of the nodes (Text-fig. 17) achieve bootstrap values in excess of 50 per cent.: nodes 2 (72 per cent.) and 11 (68 per cent.) This offers some measure of confidence in the reality of the clade containing Prolacertiformes and *Trilophosaurus* (node 2) and the clade consisting of *Tanystropheus longobardicus* and *Tanytrachelos* (node 11). All other branching points in the favoured tree (Text-fig. 17) require further investigation.

The effects of the safe deletion procedures are dramatic. When analyses were performed with the full data set (Table 3), PAUP ran for more than 2 weeks on a Macintosh Power PC, and still did not complete the analysis. With the three redundant taxa, *Tanystropheus antiquus*, *T. fossai* and *Rhombopholis*, deleted, the run lasted for less than 30 minutes (Text-fig. 16), and the final RAC run (Text-fig. 17) lasted for 2·03 seconds.

Clade definitions

Many of the characters used in the analysis have variable distributions across the favoured cladogram (Text-fig. 17), and they do not define any clades uniquely (characters 2–3, 5, 15, 18, 31–35, 38–41, 43, 45). Characters 13, 29 and 30 are autapomorphic. Certain characters define nodes as follows (these are assigned to the smallest possible clade, and some might turn out to define larger clades when more complete material is available).

Node 1: ?4 (pineal foramen reduced or absent; also in *Tanytrachelos*); 16 (pterygoid flange teeth absent; also in *Tanytrachelos*); ?28 (radius 40–65 per cent. length of humerus; also in *Tanytrachelos*).
Node 2: 23 (neural spines of dorsal vertebrae tall and rectangular; reversed in *Langobardisaurus*).
Node 3: ?1 (dorsomedial process of premaxilla reduced; also in *T. longobardicus*); 10 (posterior process of jugal absent; also in *Macrocnemus*); 14 (posterior dentary teeth lie anterior to posterior maxillary teeth).
Node 4: Prolacertiformes: 11 (quadratojugal tall and with reduced anterior process); 17 (more than seven cervical vertebrae); 19 (mid and posterior cervical centra longer than dorsals); 20 (cervical neural spine long and low); 22 (cervical ribs long and slender).
Node 5: 45 (metatarsal 4 more than three times length of metatarsal 5).
Node 6: 24 (trunk intercentra absent).
Node 7: 26 (scapula low and subequal in size to coracoid); 27 (entepicondylar groove or foramen on humerus absent; reversed in *Tanytrachelos*); 36 (thyroid foramen in pelvis); 37 (pubis narrow and waisted; reversed in *Cosesaurus*).
Node 8: 21 (ovoid spine table on top of neural spine; also in *Boreopricea*); 44 (second distal tarsal absent).
Node 9: 9 (ventral ramus of squamosal reduced and cotyle formed for quadrate head); 32 (metacarpal 3 is equal in length to, or longer than, metacarpal 4; also in *Boreopricea*); 43 (first distal tarsal absent); 46 (metatarsal 5 symmetrical and very short); 47 (second phalanx on digit 5 of foot long; also in *Boreopricea*).
Node 10: Tanystropheidae: 7 (postfrontal is a short element lacking processes); 12 (quadratojugal absent).
Node 11: 6 (lacrimal restricted to the orbital rim in lateral view); 18 (ten or more cervical vertebrae); 25 (ribs fused to posterior dorsal vertebrae; also in *Langobardisaurus*); 42 (pes centrale absent); 48 (postcloacal bones present).

REFERENCES

BARTHOLOMAI, A. 1979. New lizard-like reptiles from the early Triassic of Queensland. *Alcheringa*, **3**, 225–234.

BASSANI, F. 1886. Sui fossili e sull'età degli schisti bituminosi triasici di Besano in Lombardia. *Atti della Società Italiana di Scienzi Naturali*, **29**, 15–72.

BENTON, M. J. 1983. The Triassic reptile *Hyperodapedon* from Elgin: functional morphology and relationships. *Philosophical Transactions of the Royal Society of London, Series B*, **302**, 605–720.

——— 1984. The relationships and early evolution of the Diapsida. 575–596. *In* FERGUSON, M. W. J. (ed.). *The structure, development, and evolution of the reptiles*. Zoological Society of London, London, 697 pp.

——— 1985. Classification and phylogeny of the diapsid reptiles. *Zoological Journal of the Linnean Society*, **84**, 97–164.

——— 1990. The species of *Rhynchosaurus*, a rhynchosaur (Reptilia, Diapsida) form the Middle Triassic of England. *Philosophical Transactions of the Royal Society of London, Series B*, **328**, 213–306.

——— and WALKER, A. D. 1996. *Rhombopholis*, a prolacertiform reptile from the Middle Triassic of England. *Palaeontology*, **39**, 763–782.

BROILI, F. and FISCHER, E. 1916. *Trachelosaurus Fischeri* nov. gen. nov. sp. Ein neuer Saurier aus dem Buntsandstein von Bernburg. *Jahrbuch der Königlichen Preussischen Geologischen Landesanstalt*, **37**, 359–414.

CALZAVARA, M., MUSCIO, G. and WILD, R. 1980. *Megalancosaurus preonensis* n.g., n.sp., a new reptile from the Norian of Friuli. *Gortania*, **2**, 49–64.

CAMP, C. L. 1945. *Prolacerta* and the protorosaurian reptiles. Parts I, II. *American Journal of Science*, **243**, 17–32, 84–101.

CHATTERJEE, S. K. 1980. *Malerisaurus*, a new eosuchian reptile from the late Triassic of India. *Philosophical Transactions of the Royal Society of London, Series B*, **291**, 163–200.

——— 1986. *Malerisaurus langstoni*, a new diapsid from the Triassic of Texas. *Journal of Vertebrate Paleontology*, **6**, 297–312.

COLBERT, E. H. 1987. The Triassic reptile *Prolacerta* in Antarctica. *American Museum Novitates*, **2882**, 1–14.

CRUICKSHANK, A. R. I. 1972. The proterosuchian thecodonts. 89–119. *In* JOYSEY, K. A. and KEMP, T. S. (eds). *Studies in vertebrate evolution*. Oliver & Boyd, Edinburgh, 284 pp.

ELLENBERGER, P. 1977. Quelques précisions sur l'anatomie et la place systématique très spéciale de *Cosesaurus aviceps*. *Cuadernos Geologia Ibérica*, **4**, 169–188.

EVANS, S. E. 1986. The braincase of *Prolacerta broomi* (Reptilia: Triassic). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **173**, 181–200.

——— 1988. The early history and relationships of the Diapsida. 221–260. *In* BENTON, M. J. (ed.). *The phylogeny and classification of the tetrapods. Volume 1. Amphibians, reptiles, birds*. Systematics Association Special Volume, 35A. Clarendon Press, Oxford, 377 pp.

FRASER, N. C. and BENTON, M. J. 1989. The Triassic reptiles *Brachyrhinodon* and *Polysphenodon* and the relationships of the sphenodontids. *Zoological Journal of the Linnean Society*, **96**, 413–445.

GOW, C. E. 1975. The morphology and relationships of *Youngina capensis* Broom and *Prolacerta broomi* Parrington. *Palaeontologia Africana*, **18**, 89–131.

GREGORY, J. T. 1945. Osteology and relationships of *Trilophosaurus*. *Publication of the University of Texas*, **4401**, 273–359.

HUENE, F. von 1908. Über die Trias-Dinosaurier Europas. *Zeitschrift der Deutschen Geologischen Gesellschaft*, **57**, 345–349.

——— 1946. Die grossen Stämme der Tetrapoden in den geologischen Zeiten. *Biologisches Zentralblatt*, **65**, 268–275.

KUHN-SCHNYDER, E. 1962. Ein weiterer Schädel von *Macrocnemus bassani* Nopcsa aus der anisischen Stufe der Trias des Monte San Giorgio (Kt. Tessin, Schweiz), *Paläontologische Zeitschrift, H. Schmidt Festband*, 110–133.

LAURIN, M. 1991. The osteology of a Lower Permian eosuchian from Texas and a review of diapsid phylogeny. *Zoological Journal of the Linnean Society*, **101**, 59–95.

MEYER, H. von 1847–55. *Die Saurier des Muschelkalkes mit Rücksicht auf die Saurier aus Buntem Sandstein und Keuper*. Heinrich Keller, Frankfurt-am-Main, 167 pp.

——— 1856. *Saurier aus dem Kupferschiefer der Zechstein-Formation*. Heinrich Keller, Frankfurt-am-Main, 28 pp.

NOPCSA, F. 1930. Notizen über *Macrocnemus Bassanii* nov. gen. et spec. *Centralblatt für Mineralogie, Geologie, und Paläontologie*, **1930**, 252–255.

OLSEN, P. E. 1979. A new aquatic eosuchian from the Newark Supergroup (Late Triassic–Early Jurassic) of North Carolina and Virginia. *Postilla*, **176**, 1–14.

ORTLAM, D. 1967. Fossile Böden als Leithorizonte für die Gliederung des Höheren Buntsandsteins im nördlichen Schwarzwald und südlichen Odenwald. *Geologisches Jahrbuch*, **84**, 485–590.

OSBORN, H. F. 1903. The reptilian subclasses Diapsida and Synapsida and the early history of the Diaptosauria. *Memoirs of the American Museum of Natural History*, **1**, 449–507.

OWEN, R. 1842. Description of parts of the skeleton and teeth of five species of the genus *Labyrinthodon* (*Lab. leptognathus*, *Lab. pachygnathus* and *Lab. ventricosus*, from the Coton-end and Cubbington Quarries of the Lower Warwick Sandstone; *Lab. Jaegeri*, from Guy's Cliff, Warwick; and *Lab. scutulatus*, from Leamington); with remarks on the probable identity of the *Cheirotherium* with this genus of extinct batrachians. *Transactions of the Geological Society, London*, (2), **6**, 515–543.

PARRINGTON, F. R. 1935. On *Prolacerta broomi*, gen. et sp. n., and the origin of lizards. *Annals and Magazine of Natural History*, Series 10, **16**, 197–205.

PEYER, B. 1937. Die Triasfauna der Tessiner Kalkalpen. XII. *Macrocnemus bassani* Nopcsa. *Abhandlungen der Schweizerischen Paläontologischen Gesellschaft*, **59**, 1–140.

RENESTO, S. 1991. The anatomy and relationships of *Endennasaurus acutirostris* (Reptilia, Neodiapsida), from the Norian (Late Triassic) of Lombardy. *Rivista Italiana di Paleontologia i Stratigrafia*, **97**, 409–430.

—— 1994*a*. A new prolacertiform reptile from the late Triassic of Northern Italy. *Rivista Italiana di Paleontologia i Stratigrafia*, **100**, 285–306.

—— 1994*b*. *Megalancosaurus preonensis*, a possibly arboreal archosauromorph from the Norian (Late Triassic) of Northern Italy. *Journal of Vertebrate Paleontology*, **14**, 38–52.

RIEPPEL, O. 1989. The hind limb of *Macrocnemus bassani* (Nopcsa) (Reptilia, Diapsida): development and functional anatomy. *Journal of Vertebrate Paleontology*, **9**, 373–387.

ROMER, A. S. 1966. *Vertebrate paleontology*. Third edition. University of Chicago Press, Chicago, 468 pp.

SANZ, J. L. and LOPEZ MARTINEZ, N. 1984. The prolacertid lepidosaurian *Cosesaurus aviceps* Ellenberger & Villalta, a claimed 'protoavian' from the Middle Triassic of Spain. *Geobios*, **17**, 747–753.

SEELEY, H. G. 1888. Researches on the structure, organisation, and classification of the fossil Reptilia. 1, On *Protorosaurus speneri* (von Meyer). *Philosophical Transactions of the Royal Society of London*, **178**, 187–213.

SMITH, C.-B. 1993. The powers and pitfalls of parsimony. *Nature*, **361**, 603–607.

SWOFFORD, D. L. 1993. *PAUP, Phylogenetic Analysis Using Parsimony, version 3.1.1. Documentation and software*. Illinois Natural History Survey: Champaign, Illinois.

TATARINOV, L. P. 1978. Triassic prolacertilians of the U.S.S.R. *Paleontological Journal*, **12**, 505–514.

WILD, R. 1973. Die Triasfauna der Tessiner Kalkalpen. XXIII. *Tanystropheus longobardicus* (BASSANI)(Neue Ergebnisse). *Abhandlungen der Schweizerischen Paläontologischen Gesellschaft*, **95**, 1–162.

—— 1980. Die Triasfauna der Tessiner Kalkalpen. XXIV. Neue Funde von *Tanystropheus* (Reptilia, Squamata). *Abhandlungen der Schweizerischen Paläontologischen Gesellschaft*, **102**, 1–43.

—— and OOSTERINK, H. 1984. *Tanystropheus* (Reptilia: Squamata) aus dem Unteren Muschelkalk von Winterswijk, Holland. *Grondboor en Hamer*, **5**, 142–148.

WILKINSON, M. 1992. Consensus, compatibility and missing data in phylogenetic inference. Unpublished PhD thesis, University of Bristol.

—— 1994. Common cladistic information and its consensus representation: reduced Adams and reduced cladistic consensus trees and profiles. *Systematic Biology*, **43**, 343–368.

—— and BENTON, M. J. 1996. Sphenodontid phylogeny and the problems of multiple trees. *Philosophical Transactions of the Royal Society of London*, Series B, **351**, 1–16.

YOUNG, C. C. 1973. [*Prolacertoides jimusarensis*]. *Vertebrata Palasiatica*, **2**, 46–48.

MICHAEL J. BENTON

JACKIE L. ALLEN

Department of Geology
University of Bristol
Bristol BS8 1RJ, UK